INDICATIONS OF POSSIBLE MID-CENOZOIC HYBRIDIZATION IN THE ASPENS OF THE COLUMBIA PLATEAU

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Trembling aspen, *Populus tremuloides* Michaux, is the most widely distributed tree species in North America (Strothmann and Zasada 1957). Although several species and varieties of western aspens have been recognized, *Populus tremuloides* Michx. for many years has been the accepted name embracing this genetically variable taxon (Little 1953). One would expect major physiological differences and some related morphological differences throughout its vast range; an indication of the former is given by Pauley, Johnson, and Santamour (1963). They reported the results of a seed source experiment of aspens initiated in 1950-1952 in eastern Massachusetts, in which aspens from the Northeastern States, Lake States, Northern, Central, and Southern Rocky Mountains, Washington, and the Yukon territory were compared. Although the initial survival percentage was acceptable to high (41-100%), all western sources exhibited slow growth and were clearly ill-adapted to the environment of Weston, Massachusetts. Only 2 of the 549 individuals were alive in 1962. This experiment suggested that surprising differences may exist between western and eastern aspens.

The purpose of this paper is to introduce other evidence indicating that certain individuals as well as a population of aspen from the Columbia Plateau[1] may not be as closely related to eastern quaking aspen as we have tacitly assumed. Two clones of quaking aspen from northern Idaho resembling hybrids between *P. grandidentata* and *P. tremuloides*

[1]For purposes of this paper, the "Columbia Plateau," because of its relevance in mid-Cenozoic geology and flora, is used to designate the general area from which the author's collections and *Populus* fossils collected by numerous investigators were made. As used here it embraces what are now parts of California, Nevada, Oregon, Washington, Idaho, and Montana (Fenneman 1931).

in Lower Michigan are hereinn described. Morphological differences between a group of aspen clones from northern Idaho, Washington, and western Montana, considered here as part of the eastern edge of the Columia Plateau, are compared and contrasted with clones from Michigan.

METHODS AND MATERIALS

During the summers of 1959 and 1960 collections of leaves and twigs of aspen clones for a personal study herbarium were made in northern Idaho, western Montana, and Washington as time and circumstances permitted. Observations of growth habit, phenology, and sex were also made. Opportunities for detailed study of the leaf and twig samples were delayed until March of 1966 when I had returned to the University of Michigan and resumed the investigations of natural hybridization in the aspens. Examination of the clones of the western specimens led to an unexpected discovery, namely that two of the western clones were evidently hybrids between *P. grandidentata* and *P. tremuloides* in leaf and bud characteristics. This discovery prompted a systematic study of 30 western clones sampled.

The early leaves from the central portion of shoots 1-3 in long were selected and the blade width and length, petiole length, and number of teeth per leaf side were determined. Up to 20 leaves were taken per clone for measurement; the average number was 18. The terminal buds of at least four shoots of each clone were examined and the presence and distribution of pubescence observed and recorded. Comparisons were made between these western clones and the bigtooth and quaking aspen clones sampled in northern Michigan (Barnes 1959). The latter group consisted of 21 bigtooth clones and 31 trembling aspen clones growing on two sites. Means of blade width and length, petiole length, and number of teeth for the two groups are not entirely comparable due to minor differences in sampling. However, the site differences are so great that only very general comparisons of leaf size can be made in any event. Number of teeth and pubescence on terminal buds have proved to be more reliable characteristics, and are thus apparently better phenotypic indicators of hybridity in Michigan aspens than

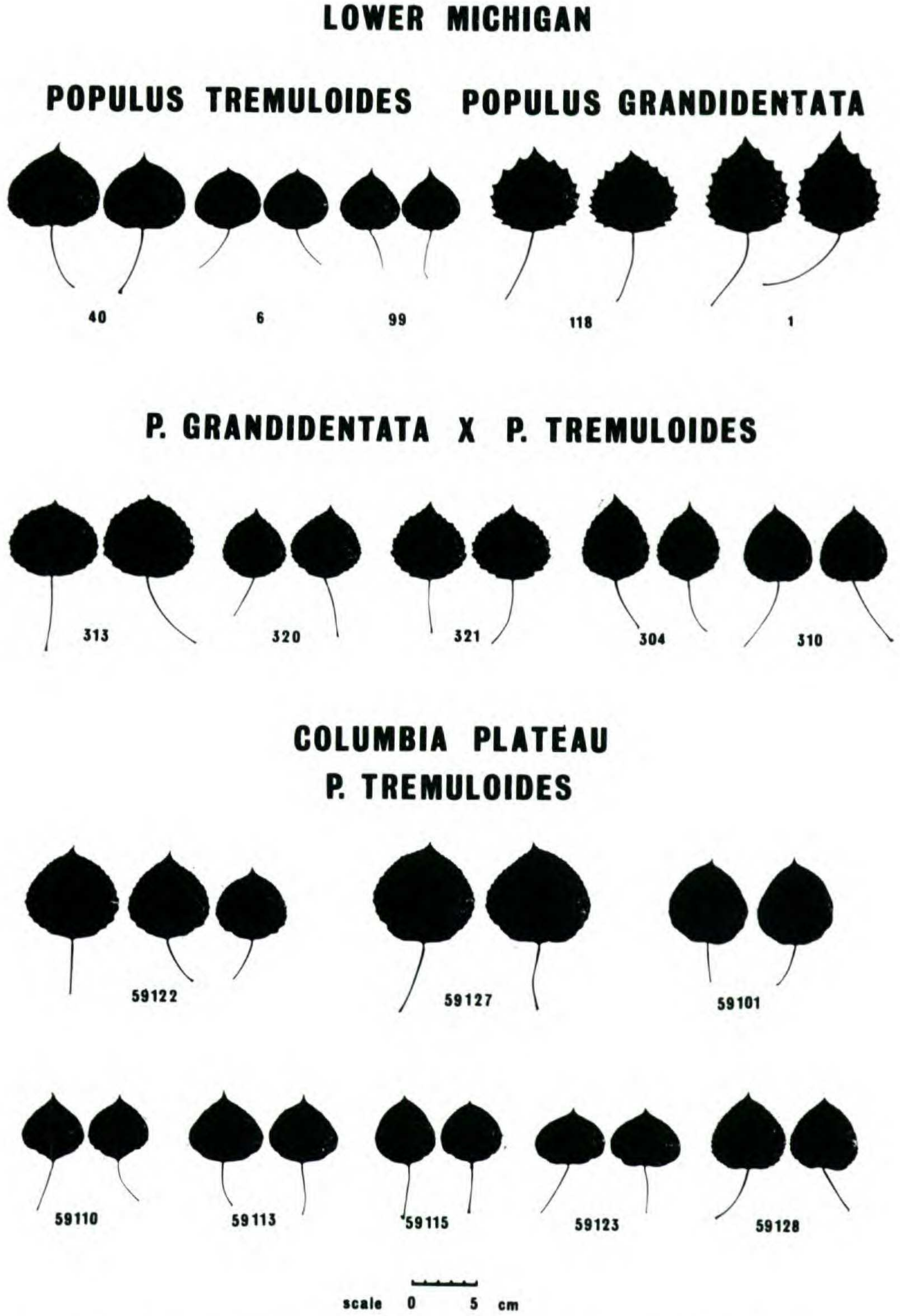

Fig. 1. Comparison of leaf size, shape and dentation of *P. grandidentata*, *P. tremuloides* and hybrids between them from Lower Michigan and "*P. tremuloides*" from the Columbia Plateau.

the leaf dimensions. Pubescence of buds collected Aug. 10-13, 1966 was studied on 50 clones of quaking aspen in Iron Co. and 20 clones in Washtenaw Co., Michigan.

RESULTS AND DISCUSSION

Silhouettes of leaves from the central portion of shoots from clones 59122 and 59127 from Kootenai County, Idaho are illustrated in Fig. 1 (lower left). Representative leaves of Lower Michigan *P. tremuloides*, *P. grandidentata*, and natural hybrids[2] between them and leaves from six clones of quaking aspen from Idaho and Washington are also shown. It will be noted that Idaho clones 59122 and 59127 are like various natural hybrids in Michigan (Fig. 1). Although the Michigan hybrids exhibit great morphological variability, the most consistent diagnostic morphological characters are those of tooth number and bud pubescence which in presumed F_1 hybrids are approximately intermediate between those of the parents. There is, however, considerable variation even in these traits, and it is not yet known what amount of variation in these traits is attributable to maternal effects, introgression, and additive and non-additive gene action. For the aspens studied in Lower Michigan the average number of teeth of *P. grandidentata* clones was approximately 10, natural hybrids 18, and *P. tremuloides* 30. Means and ranges of tooth number and the means of leaf dimensions of the respective populations are presented in Table 1.

Populus grandidentata exhibited dense pubescence on all bud scales. Terminal buds in winter condition of *P. tremuloides* of Lower Michigan sites were glabrous except for rare clones having minute pubescence on the basal scales. Nearly all the terminal buds from the 70 clones collected in mid-August 1967 exhibited sparse pubescence on the upper portion of the basal bud scales. Many *P. tremuloides* clones showed bud scales which have ciliate margins. Natural hybrids have pubescence on almost all bud scales but it is usually much less dense than in *P. grandidentata;* the

[2]The term "natural hybrid" is used here to include F_1 hybrids, later generation segregates and introgressants; we are as yet unable to determine precisely the parentage of each hybrid clone.

pubescence tends to become more dense on the basal scales.

Using leaf dimensions and morphology, and bud characteristics, one would be clearly unable to separate the two Idaho clones (59122 and 59127, Fig. 1) from natural aspen hybrids of Lower Michigan. The average number of teeth per leaf side of both western clones was 19.5. The average tooth number of 25 natural Michigan hybrids reported by Barnes (1961) was 17.6. The Idaho clones had moderate to dense pubescence on the lower terminal bud scales, and in 59122 the pubescence extended downward completely coating the shoot produced the year of collection. No pubescence was observed on the upper bud scales except for a few fine hairs along their margins. This condition is somewhat different from most Lower Michigan hybrids. The latter typically have fine pubescence on both lower and upper bud scales. In pubescence the two Idaho clones closely resembled the putative introgressant Michigan clone 310, but both western clones had markedly fewer teeth (Fig. 1).

The most striking difference between all of the Michigan and the specimens of western trembling aspens was the presence of moderate to dense pubescence on the basal scales of terminal buds of all clones of the latter. Some western clones exhibited pubescence not only on lower scales but the upper as well. Furthermore, clone 59108 exhibited pubescence on the shoots produced the year the collection was made. This feature has never been reported or observed for immature or mature shoots of any eastern *P. tremuloides*. All of the western collections were made in July, August, or September, so that this apparently was not merely juvenile pubescence which would disappear later. The axillary buds, where present, were also pubescent on the lower scales, but to a lesser degree than on terminal buds.

It is unknown to what extent aspen clones of the Columbia Plateau or other geographic regions of the West exhibit pubescent buds. At the request of the author, Mr. R. Dennis Harr sent a sample of buds from eight clones of quaking aspen from Larimer County, Colorado. Terminal buds of these clones were much more glabrous than those

of the Columbia Plateau collections, but two did have a moderate amount of pubescence on the lower scales. Minute pubescence was also found on lower terminal bud scales on most of the Colorado specimens. Terminal buds of Lower Michigan quaking aspens were even less pubescent. The Colorado and Michigan collections seem more alike than are the Colorado and Columbia Plateau clones.

A comparison of the leaf dimensions and tooth number per leaf side of 30 western clones and the Lower Michigan clones in Table 1 indicates no major or systematic difference between them. Leaf dimensions are apparently highly influenced by the local environment, and hence clones from sites in both regions should be grown under controlled conditions to assess the differences. Tooth number is probably somewhat less susceptible to environmental modification. Tooth number, however, is positively correlated with leaf size. The correlation coefficient of the relationship between leaf area and tooth number of *P. tremuloides* on the Pellston plain site (indicated in Table 1) was significant, $r = .65$ ($P<.05$). Also, the size of leaves and number of teeth of clones on the Moraine site are larger than the respective attributes of clones on the Pellston plain. Since tooth numebr is positively correlated with leaf size one might expect the western clones, the leaf sizes of which are larger, to have as many or more teeth than the clones from the Michigan sites. However, the number of teeth of the western clones was somewhat less (25.3) than that of clones from both of the Michigan sites (30.5). The difference was not statistically significant ($P>.40$) because of the great variation within both groups. These data do indicate, however, that some clones have markedly larger and fewer teeth than would typically be expected of Michigan *P. tremuloides;* other clones exhibited no difference whatsoever. Obviously, systematic studies throughout the range of *P. tremuloides* coupled with progeny tests under controlled conditions are needed to evaluate the differences and determine their causes.

Although the western clones were originally sampled and cursorily identified as typical of eastern *P. tremuloides*,

systematic differences are now clearly evident. Descriptions of western aspens in floras and dendrology texts provide no evidence of differences in pubescence of the buds (Jepson, 1909; Kirkwood, 1930; Longyear, 1927; Preston, 1940; Sudworth, 1908). Illustrations of western aspen leaves, however, do indicate the lower tooth numbers discussed. Sudworth (1908), for example, illustrated both an eastern *P. tremuloides* and a western *P. tremuloides* from Colorado. Number of teeth per leaf side of the eastern aspen was approximately 33 in contrast to about 22 for the Colorado aspen. This, however, might be due to chance sampling of clones not representative of the populations.

How can we account for the observed differences between the western and Michigan populations of quaking aspen? One explanation would be clinal evolutionary differentiation along gradients running from west to east. Another hypothesis is hybridization and flow of genes from a western taxon or taxa having pubescent buds and few large teeth into the mid-Cenozoic quaking aspen. It is not the purpose of this paper to attempt an answer to this question through lengthy speculative arguments. However, a brief review of the taxonomy of western aspens is made below and some evidence indicating that hybridization of aspens could have taken place in the Columbia Plateau is presented.

The western aspen, *P. aurea*, was described by Tidestrom (1911) as a species which "formed forests throughout Colorado, Utah, and adjoining territory. . . ." This taxon differed from *P. tremuloides* Michaux in floral characteristics and in the fall coloration of leaves. The leaves were described as serrate and the buds ("gemmis") were termed glabrous, gummy, and conical. Other authors doubted the validity of this taxon (Daniels, 1911; Preston, 1940; Clokey, 1951) and it was subsequently considered synonymous with *P. tremuloides* Michx. by Little (1953). The plants originally described by Tidestrom were from the central and southern Rockies and may be more closely related to eastern *P. tremuloides* than the populations in the Columbia Plateau. The collections by Harr having buds somewhat

similar to Michigan populations of *P. tremuloides* tend to support this.

Tidestrom (Piper and Beattie 1915) also recognized another species, *P. vancouveriana* Trelease. He distinguished this species from eastern *P. tremuloides* and western *P. aurea* by the "peculiar dentition of the leaves. The teeth are much larger than in any of its immediate allies and besides being crenulate are depressed so that each tooth viewed from the edge forms a double curve." The number of teeth was not reported. The buds were described as "smooth, conical, gummy, dark purple." Without examination of the type specimen it is difficult to draw any firm conclusions about the extent to which this taxon resembles clones of the Columbia Plateau.

One explanation for the existence of the larger-toothed, pubescent Idaho clones is that they are recent hyrids or introgressants between western *P. tremuloides* and the eastern *P. grandidentata*. The westernmost occurrence of *P. grandidentata* is in southeastern Manitoba (Slabaugh 1958). Thus the nearest localities are about 1,000 miles northeast of the Idaho "*P. tremuloides*" clones. Since *P. grandidentata* sheds pollen later than *P. tremuloides* where the two are sympatric and under the prevailing westerlies, this hypothesis seems most unlikely.

Another possibility is that there were situations in the mid-Cenozoic period parallel to the ones now taking place commonly in the southern part of Lower Michigan — conditions promoting natural hybridization and introgression between *P. grandidentata* and *P. tremuloides*. This hypothesis would necessitate the existence of a western taxon similar to the present-day eastern *P. tremuloides* in having many teeth and essentially glabrous buds, and the contemporaneous presence of a large-toothed aspen with pubescent buds like those of *P. grandidentata*.

During the Miocene period, a mixed deciduous forest, the "Arcto-Tertiary Geoflora," characterized the Columbia Plateau (Chaney 1959). Several species of *Populus*, at least two of which were aspens, i.e., members of Section Leuce, flourished in this region together with beech, maples, oaks,

ashes, and willows. An aspen leaf termed *Populus lindgreni* Knowlton by LaMotte (1936)[3] and a leaf described by Chaney and Axelrod (1950)[4] as *Populus washoensis* Brown both closely resemble the leaves of modern *P. grandidentata*. Chaney and Axelrod (1959) considered the *Populus lindgreni* Knowlton as illustrated by LaMotte (1936) to be synonymous with *P. washoensis* Brown. The leaf named *P. voyana* by Chaney and Axelrod (1959)[5] is similar to leaves of modern *P. tremuloides*. Thus, if the two aspens were sympatric, hybridization might have taken place and some genes from the large-toothed aspen became incorporated in the populations of trembling aspen of the Columbia Plateau. After some hybridization between these species, extinction of the typical large-toothed aspen member took place along with most of the other mesophytic members of the community due to the rise of the Cascade Mountains. Further gene exchange was thus prevented so that unless first generation hybrids have been perpetuated asexually, the present quaking aspen clones could be introgressants possessing some genes of the fossil species.

Before accepting the above hypothesis, other facts should be investigated. Besides such leaves as resemble the modern *P. grandidentata*, the fossil record also exhibits a variety of leaves of the genus *Populus* which have been termed *Populus eotremuloides* Knowlton and *P. lindgreni* Knowlton.

These Chaney and Axelrod (1959) considered to be closely related to *P. balsamifera* and *P. heterophylla*, respectively. Most of the specimens illustrated by Chaney (1959), LaMotte (1936), and Smith (1941) do not resemble typical modern *P. tremuloides* of Michigan. Their illustrations resemble *P. tremula* and hybrids similar to those between Michigan *P. grandidentata* and *P. tremuloides*. The array of forms, including early leaves, late leaves, and leaves from

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[3]Plate 4, Fig. 1. *Populus lindgreni* Knowlton. Pleisotype. U.C. Mus. Palaeobot., No. 956.

[4]Plate 18, Fig. 7. *Populus washoensis* Brown. Hypotypes U.C.M.P., Paleobot. Coll. No. 2927. Blue Mountains.

[5]Plate 18, Fig. 4. *Populus voyana* Chaney and Axelrod. Hypotype, U.C.M.P., Paleobot. Coll. No. 562. Trout Creek.

Table 1. Leaf dimensions and number of teeth on leaves of aspen clones from Michigan and Idaho, Montana and Washington.

Taxon	Location	Number of Clones	Leaf Dimension in cm			Number of Teeth per leaf side	
			Blade Width	Blade Length	Petiole Length	Mean	Range
P. grandidentata	Michigan, Moraine site[1]	18	7.1	8.1	5.8	10.4	7-13
P. tremuloides	Michigan, Moraine site	10	5.1	4.8	3.8	32.7	28-36
P. tremuloides	Michigan, Pellston plain site[2]	21	4.2	4.5	3.3	29.4	22-39
P. tremuloides	Lower Michigan[3]	31	4.5	4.6	3.5	30.5	22-39
P. tremuloides	Northern Idaho, western Montana, Washington	30	5.0	5.3	3.9	25.3	19-33

[1]SE¼, Section 6, T36N, R3W, Cheboygan County, Michigan.

[2]S½, Section 25 and N½, Section 36, T37N, R4W, Emmet County, Michigan.

[3]Clones from Moraine and Pellston plain sites combined.

Table 1. Leaf dimensions and number of teeth on leaves of aspen clones from Michigan and Idaho, Montana and Washington.

various positions along the shoot, indicate a need for thorough study of *Populus* species in the Arcto-Tertiary-Geoflora of the Columbia Plateau and their relationships to aspens of other regions of the West, as well as those of eastern North America. The Asian race of *P. tremula*, known as *P. tremula* var. *davidiana* Schneider and a taxon resembling the Asian aspen with pubescent buds, *P. sieboldii* Miq., may also have been in the Arcto-Tertiary-Geoflora. Graham (1965) reported that leaves of *P. washoensis* Brown resemble both *P. grandidentata* and the *P. tremula* of eastern Asia. Thus, the aspens of the Columbia Plateau may be the progeny of a complex of several related species whose influence may yet be tracable through biosystematic studies.

Another important problem to be resolved is the time and circumstances of hybridization if, in fact, such did occur. Did it occur before the Arcto-Tertiary Geoflora reached the Columbia Plateau, or did it occur initially in Miocene times in the Columbia Plateau when conditions were such that gene exchange was possible? Finally, the possibility of actual existence of a large-toothed, pubescent aspen in modern-day stands having relicts of this Miocene flora should be explored.

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